Potential for Using Multivariate Autoregressive Models to Investigate Dynamics of British Columbia Groundfish Communities, Including Appraisal of the LAMBDA Software Package

S.J. Keightley, A.M. Edwards, and C.A. Holt

Fisheries and Oceans Canada
Pacific Biological Station
3190 Hammond Bay Road
Nanaimo, British Columbia
V9T 6N7, Canada

2011

Canadian Technical Report of
Fisheries and Aquatic Sciences 2968

Canadian Technical Report of Fisheries and Aquatic Sciences

Technical reports contain scientific and technical information that contributes to existing knowledge but which is not normally appropriate for primary literature. Technical reports are directed primarily toward a worldwide audience and have an international distribution. No restriction is placed on subject matter and the series reflects the broad interests and policies of Fisheries and Oceans Canada, namely, fisheries and aquatic sciences.

Technical reports may be cited as full publications. The correct citation appears above the abstract of each report. Each report is abstracted in the data base *Aquatic Sciences and Fisheries Abstracts.*

Technical reports are produced regionally but are numbered nationally. Requests for individual reports will be filled by the issuing establishment listed on the front cover and title page.

Numbers 1-456 in this series were issued as Technical Reports of the Fisheries Research Board of Canada. Numbers 457-714 were issued as Department of the Environment, Fisheries and Marine Service, Research and Development Directorate Technical Reports. Numbers 715-924 were issued as Department of Fisheries and Environment, Fisheries and Marine Service Technical Reports. The current series name was changed with report number 925.

Rapport technique canadien des sciences halieutiques et aquatiques

Les rapports techniques contiennent des renseignements scientifiques et techniques qui constituent une contribution aux connaissances actuelles, mais qui ne sont pas normalement appropriés pour la publication dans un journal scientifique. Les rapports techniques sont destinés essentiellement à un public international et ils sont distribués à cet échelon. II n'y a aucune restriction quant au sujet; de fait, la série reflète la vaste gamme des intérêts et des politiques de Pêches et Océans Canada, c'est-à-dire les sciences halieutiques et aquatiques.

Les rapports techniques peuvent être cités comme des publications à part entière. Le titre exact figure au-dessus du résumé de chaque rapport. Les rapports techniques sont résumés dans la base de données *Résumés des sciences aquatiques et halieutiques.*

Les rapports techniques sont produits à l'échelon régional, mais numérotés à l'échelon national. Les demandes de rapports seront satisfaites par l'établissement auteur dont le nom figure sur la couverture et la page du titre.

Les numéros 1 à 456 de cette série ont été publiés à titre de Rapports techniques de l'Office des recherches sur les pêcheries du Canada. Les numéros 457 à 714 sont parus à titre de Rapports techniques de la Direction générale de la recherche et du développement, Service des pêches et de la mer, ministère de l'Environnement. Les numéros 715 à 924 ont été publiés à titre de Rapports techniques du Service des pêches et de la mer, ministère des Pêches et de l'Environnement. Le nom actuel de la série a été établi lors de la parution du numéro 925.

Canadian Technical Report of

Fisheries and Aquatic Sciences 2968

2011

Potential for Using Multivariate Autoregressive Models to Investigate Dynamics of British Columbia Groundfish Communities, Including Appraisal of the LAMBDA Software Package

by

S.J. Keightley, A.M. Edwards, and C.A. Holt

Fisheries and Oceans Canada
Pacific Biological Station
3190 Hammond Bay Road
Nanaimo, British Columbia
V9T 6N7, Canada

*Contact author: Andrew.Edwards@dfo-mpo.gc.ca

Cat. No. Fs97-6/2968E ISSN 0706-6457

Correct citation for this publication:

Keightley, S.J., Edwards, A.M., and Holt, C.A. 2011. Potential for using multivariate autoregressive models to investigate dynamics of British Columbia groundfish communities, including appraisal of the LAMBDA software package. Can. Tech. Rep. Fish. Aquat. Sci. 2968: iv + 24 p.

ABSTRACT

Keightley, S.J., Edwards, A.M., and Holt, C.A. 2011. Potential for using multivariate autoregressive models to investigate dynamics of British Columbia groundfish communities, including appraisal of the LAMBDA software package. Can. Tech. Rep. Fish. Aquat. Sci. 2968: iv + 24 p.

Multivariate autoregressive (MAR) models are a relatively new modelling technique, and are used in ecology to estimate interactions between multiple biotic and abiotic factors within an ecosystem. Initial applications have focussed on freshwater systems. Recently, MAR models have been constructed to examine marine community dynamics. This technical report explores how MAR models could be applied to time series for groundfish populations along the coast of British Columbia, Canada. As a pilot study, we implemented MAR models, using information on ocean conditions and estimates of recruitment from stock assessments, to investigate recruitment patterns for four species of groundfish: Pacific ocean perch *Sebastes alutus*, canary rockfish *S. pinniger*, Pacific hake *Merluccius productus* and sablefish *Anoplopoma fimbria*. MAR models were implemented using the software package LAMBDA. While there are similarities between published hypotheses for drivers of recruitment and our outputs from LAMBDA for the species investigated, we are apprehensive in making generalizations about the usefulness of the LAMBDA software applied to recruitment time series. For future work, we recommend looking into the state-space approaches currently under development. These approaches can better incorporate estimates of uncertainty that are routinely calculated in groundfish stock assessments.

RÉSUMÉ

Keightley, S.J., Edwards, A.M., and Holt, C.A. 2011. Potential for using multivariate autoregressive models to investigate dynamics of British Columbia groundfish communities, including appraisal of the LAMBDA software package. Can. Tech. Rep. Fish. Aquat. Sci. 2968: iv + 24 p.

Les modèles multivariables à vecteurs autorégressifs (MMVA) représentent une technique de modélisation relativement nouvelle qui est utilisée en écologie pour estimer les interactions entre les multiples facteurs biotiques et abiotiques au sein d'un écosystème. Les applications initiales ont porté essentiellement sur les écosystèmes d'eau douce. Récemment, des MMVA ont été établis pour examiner les forces dynamiques de l'écosystème marin. Le présent rapport technique examine la façon dont on pourrait appliquer les MMVA aux séries chronologiques relatives aux poissons de fond le long du littoral de la Colombie-Britannique, au Canada. Dans le cadre d'une étude pilote, nous avons mis en application des MMVA, en utilisant les données sur les conditions océaniques et les estimations de recrutement provenant des évaluations de stocks, en vue d'étudier les régimes de recrutement pour quatre espèces de poissons de fond : le sébaste à longue mâchoire *Sebastes alutus*, le sébaste canari *Sebastes pinniger*, le merlu du Pacifique *Merluccius productus* et la morue charbonnière *Anoplopoma fimbria*. Les MMVA ont été mis en application au moyen du logiciel LAMBDA. Bien qu'il y ait des similitudes entre les hypothèses publiées relativement aux facteurs de recrutement et nos extrants issus du logiciel LAMBDA pour les espèces à l'étude, nous hésitons à faire des généralisations relativement à l'utilité du logiciel LAMBDA en ce qui concerne son application aux séries chronologiques de recrutement. Pour les futurs travaux, nous recommandons d'examiner les approches de type état-espace en voie d'élaboration. Ces approches tiennent mieux compte des estimations marquées d'un facteur d'incertitude, qui sont invariablement calculées dans les évaluations des stocks de poissons de fond.

PREFACE

This report was completed in partial fulfillment of the Co-operative Education requirements of the University of Victoria, and was funded by Fisheries and Oceans Canada. We thank Rowan Haigh, Greg Workman and Eric Ward for useful discussions, and Sean Cox, Robyn Forrest and Paul Starr for contributing results from stock assessments.

INTRODUCTION

Little is known about the early life stages of many groundfish species found along the coast of British Columbia. While biotic and abiotic factors during these stages certainly have an effect on recruitment, these influences, if mentioned at all, are a minor part of the stock assessments used to provide advice to fishery managers.

Related to this general situation, one of the main priorities listed in the Fisheries & Oceans Canada Five-Year Research Agenda (2007-2012) is to increase understanding of the productivity of fish populations and communities. This prioritization has led to increased investigation into factors other than fishing that could influence productivity, including potentially competing species, temperature, and oceanic indices. Elsewhere, novel population modelling techniques are also under investigation, such as multivariate autoregressive models. The concurrent development of computer software packages such as LAMBDA (described below) have facilitated such investigations (e.g. Hampton et al. 2008).

Multivariate autoregressive first-order (MAR-1) processes are becoming an increasingly popular framework for ecological modelling, having been introduced in the seminal paper by Ives et al. (2003). MAR-1 models are stochastic, non-mechanistic models that utilize time series data for species abundances and environmental variables to estimate interactions between species, and interactions between species and environmental variables (Mac Nally et al. 2010). In contrast to other techniques, MAR-1 models explicitly include multiple species and account for autocorrelation in time-series. It is also possible to estimate metrics of community stability and resilience from MAR-1 models.

Here, we outline the concept of MAR-1 models, summarise their previous uses in aquatic ecology and present some questions concerning British Columbia groundfish that they could potentially be used to investigate. We then describe the LAMBDA software, and describe our use of it to investigate possible environmental drivers of groundfish recruitment, as a pilot study to determine the suitability of the software. We use output from four recent stock assessments, and conclude with recommendations for future analyses.

MULTIVARIATE AUTOREGRESSIVE MODELS

The following equations from Ives et al. (2003) give the essential details of MAR-1 processes – see that paper for further details. The Gompertz equation, the basis for a MAR-1 model, is an exponential equation that describes fluctuations in population abundance as

$$N_t = e^a N_{t-1}^b, \tag{1a}$$

or

$$N_t = e^{a+(b-1)\ln N_{t-1}} N_{t-1}, \tag{1b}$$

where N_t represents the population abundance at discrete time step t, a represents the intrinsic rate of population increase, and b represents degree of density dependence. This autoregressive model is for a first-order process because N_t depends only on N_{t-1} (and not on earlier values). Taking the natural logarithm of both sides and letting X_t represent ln N_t yields a simpler, linear equation

$$X_t = a + bX_{t-1}. \tag{2}$$

The stochastic version of this equation is

$$X_t = a + bX_{t-1} + E_t, \tag{3}$$

where E_t, the process error term, accounts for unexplained variation in measurements of X_t, and is assumed to be a random normal variable, independent through time, with a mean of zero and variance of σ^2. Equation (3) is a univariate autoregressive first order (AR-1) process.

The effect of a covariate (such as an environmental factor) can also be added by specifying the covariate's value as U_t, and the strength of the interaction between the covariate and the population as c:

$$X_t = a + bX_{t-1} + cU_t + E_t. \tag{4}$$

To convert this model from a univariate (AR-1) model to a multivariate (MAR-1) model, the same equation is used, but the species abundances and covariates are formatted as matrices, giving

$$\mathbf{X}_t = \mathbf{A} + \mathbf{B}\mathbf{X}_{t-1} + \mathbf{C}\mathbf{U}_t + \mathbf{E}_t. \tag{5}$$

In a model with p interacting species and q covariates, $\mathbf{X}_t$ is a $p \times 1$ vector of population abundances at time t, $\mathbf{A}$ is a $p \times 1$ vector of intrinsic population growth rates, $\mathbf{B}$ is a $p \times p$ matrix of species interactions whose elements b_{ij} give the effect of the abundance of species j on the per capita population growth rate of species i, $\mathbf{C}$ is a $p \times q$ covariate matrix whose elements c_{ij} give the strength of the effect of covariate j on species i, $\mathbf{U}_t$ is a $q \times 1$ vector of values for q covariates at time t, and $\mathbf{E}_t$ is a $p \times 1$ vector of process errors that has a multivariate normal distribution with mean vector 0 and covariance matrix $\mathbf{\Sigma}$ (Ives et al. 2003).

In a MAR-1 process, the changes in the population abundances from time $t-1$ to time t depend only on the population abundances at time $t-1$ and environmental disturbances occurring at time t; there are no direct effects from population abundances or environmental disturbances prior to time $t-1$ (Ives et al. 2003). Such a first-order (or Markov) process implies that there is enough information about a community contained at a single point in time that the immediate changes in species' abundances can be predicted. MAR-1 models provide relatively simple approximations of nonlinear, non-first-order processes, as they assume linear interactions among species and between species and environmental variables (Ives 1995a, b).

One advantage of MAR-1 models is that these metrics are readily estimated from the data, and offer a way to define stability in terms of properties of a stochastic model of populations within the community. Specifically, properties of community stability can be estimated from the multivariate stationary distributions of species abundances, which have a mean μ_∞ and variance-covariance matrix $\mathbf{V}_\infty$. From these parameters, the following metrics of community stability can be estimated (Ives et al. 2003):

i. The variance of the stationary distribution compared to the observed environmental variance, where the variance of the stationary distribution of a more stable system will be low compared to the observed environmental variance.

ii. The rate at which the transition distribution reaches the stationary distribution, where a more stable system approaches a stationary distribution more rapidly.

iii. The reactivity of the system (Neubert and Caswell 1997), a measure of how sensitive a community is to perturbations. This method differs from standard methods of measuring

stability that assume that a system has an equilibrium point, or well-defined "normal" state, from which deviations can be measured (Ives et al. 2003).

PREVIOUS APPLICATIONS OF MAR-1 PROCESSES IN AQUATIC ECOLOGY

Initial ecological applications of MAR-1 processes focussed on dynamics and stability properties of phytoplankton communities in freshwater systems. Freshwater plankton communities tend to have numerous interacting species (>10) that inhabit a reasonably contained system. Such communities generate the type of dataset required to implement MAR-1 algorithms (long-term, multiple species) more readily than other communities, such as marine fish communities.

In the original paper on MAR-1 analysis, Ives et al. (2003) used an existing dataset comprised of biotic and abiotic variables for three lakes to determine which environmental and inter-species processes had the greatest effect on the variability and overall stability of the planktonic communities. Similar limnological studies in Washington (Hampton et al. 2006) and Russia (Hampton et al. 2008) took advantage of long term datasets (30 years and 60 years, respectively). Much like Ives et al. (2003), Hampton et al. (2008) were concerned with determining drivers of plankton community dynamics, while for the Lake Washington dataset, the authors were interested in quantitative evidence that supported the conceptual model for the Lake Washington food web proposed by a previous study (Edmondson 1994).

More recently, two studies have applied MAR-1 processes in a marine context. Lindegren et al. (2009) used time series from 1974 to 2004 to create a stochastic food-web model for the Baltic sea. Their model reconstructed the history of Baltic cod stocks and was used to understand reasons for their collapse that occurred in the early 1990s. For their model, the authors employed a MAR-1 state-space framework to fit a model to a time series of population biomasses, fishing mortalities, and a number of biotic and abiotic variables (Lindegren et al. 2009). State-space models include separate equations for the population process and the observations of that process, and offer a way to partition the total variance of a time series of observations into observation and process variance (Holmes 2001, De Valpine and Hastings 2002, Lindley 2003, Dennis et al. 2006, Ward et al. 2010) as is often the case for fisheries stock assessments (e.g. Edwards et al. 2011). A state-space approach allowed Lindegren et al. (2010) to account for the observation error associated with spawning stock biomass estimates. Parameters were selected based on prior knowledge of their effects on fish stocks (including seasonal variation in temperatures and salinities, oxygen availability, zooplankton abundance, and productivity estimates). The final model supported *a priori* knowledge of the effects of species interactions, fishing, environmental variability and zooplankton variability on the abundance of the three species investigated (Lindegren et al. 2010).

In the second study that applied MAR-1 processes in a marine context, Mac Nally et al. (2010) developed a Bayesian implementation of the MAR-1 process to discern the main factors responsible for the declines of four species of pelagic fish found in the San Francisco Estuary. Their model included 54 relationships within the system. The response variables in their model were time series of abundances for the four fish species (measured as total mean catch per trawl) and prey biomasses. Covariates, also included in the model, are biotic and abiotic factors thought to influence the response variables but are not affected in turn by those response variables. The final model in their study supported previous conceptions about important drivers of community

dynamics, such as the negative effect of the 2‰ isohaline on calanoid copepods and Longfin smelt, and also identified a few relationships not known *a priori* (Mac Nally et al. 2010).

Prior to developing our own MAR-1 model we determined what types of ecological questions have been asked using MAR-1 models. Within this list of questions (below), several are applicable in a general marine ecology context, while others could be applied specifically to BC groundfish.

In addition to exploring plankton dynamics using MAR-1 models in a limnological example, Ives et al. (2003) argued that MAR-1 models are capable of describing ecological interactions as well as the stochastic characteristics of the dynamics they produce within many communities. According to Ives et al. (2003), MAR-1 models could be used to ask:

- How do mean species abundances change when there is a change in the mean value of one or more covariates?
- Will the composition of a community remain stable in the face of environmental fluctuations, or will species be lost?
- Which species in a community are most sensitive to a particular environmental factor?
- Which species have relatively large impacts on other species in the community?

When framed in a groundfish context, it might be possible to address questions including:

- What are the biotic and abiotic drivers of groundfish abundance?
- Are temperature, phytoplankton and zooplankton abundances strong drivers of rockfish communities?

We could also ask questions regarding large scale climate change, such as

- How will climate change affect groundfish communities in the Northeast Pacific region?
- How will mean species abundances of groundfish change when there is a change in the mean value of one or more covariates (e.g. sea surface temperature, Aleutian Low Pressure Index, salinity)?

As might be expected, the types of questions that can be asked are constrained by the data available, and, as mentioned earlier, long-term datasets with multiple species and covariates are essential.

LAMBDA SOFTWARE

LAMBDA (Long-term Assemblage MAR(1)-Based Data Analysis) is a MatLab toolkit designed to perform MAR-1 analysis by applying the framework developed by Ives et al. (2003). It is an open source software with a graphical user interface (GUI) that performs all the calculations required to estimate a MAR-1 model using time series data, as well as compute statistics and perform diagnostics (Viscido and Holmes 2010). Although the code is open source, changing it requires use of MATLAB – a stand-alone executable version that does not require MATLAB is also available, and was used here. LAMBDA partitions the multivariate time-series data into three categories:

i. *Classification variables* are those variables that indicate the date, time or another variable that organizes the data set.

ii. *Variates* are natural logs of time-series of abundance estimates for one or more populations.

iii. *Covariates* are variables that likely have an effect on one of more of the variates, but are not affected by a variate (e.g. SST is not dependant on the abundance of sablefish, therefore, SST is considered a covariate).

These variates and covariates are then used to estimate the MAR-1 model through either Conditional Least Squares (CLS) or Maximum Likelihood methods (Viscido 2007). Further explanation of the capabilities of LAMBDA is available in Viscido (2007) and Viscido and Holmes (2010).

EXPLORATION OF THE APPLICABILITY OF MAR-1 TECHNIQUES TO GROUNDFISH IN BRITISH COLUMBIA

The work presented here is a first attempt at applying MAR-1 techniques to time-series data for groundfish off the coast of British Columbia. The intentions were to investigate what sort of input data are required, to establish how to implement the analyses and to determine the ease of use of the LAMBDA software. Given the limited amount of time available for the project (four months), we consider the analyses, results and documentation here to be a pilot study for future work. Results are presented, but these should not be used to make definitive conclusions about environmental drivers of groundfish recruitment.

Initially, we aimed to apply MAR-1 techniques in a way similar to previous marine fisheries applications of MAR-1 processes. These studies used abundances of commercially exploited species, measured as spawning stock biomass (Lindegren et al. 2009) or mean biomass from surveys (Mac Nally et al. 2010) as variates. Two issues arose when we attempted to use biomass estimates from British Columbia groundfish stock assessments in our study; first, Lindegren et al. (2009) and Mac Nally et al. (2010) incorporated fishing effort, a parameter that necessitates considerably more complex models than time allowed for. Secondly, the focal species in these studies are short-lived, therefore, populations experience a high degree of inter-annual variation; it is this variability that lends itself to MAR-1 processes. Three of the four species of groundfish found along the British Columbia coast used in this study are long-lived, and, as a result, inter-annual variation in biomass is low. While their inter-annual variation in biomass is low, considerable variability occurs in recruitment for all four species. Consequently, we implemented MAR-1 processes in the software package LAMBDA to examine year-to-year variation in recruitment to try and help understand recruitment patterns described in the literature for four species of groundfish found along the British Columbia coast: Pacific ocean perch *Sebastes alutus*, canary rockfish *S. pinniger*, Pacific hake *Merluccius productus*, and sablefish *Anoplopoma fimbria*.

One caveat regarding our results and conclusions is related to the interpretation of the coefficients estimated in LAMBDA. Where previous studies have used species *population* abundances measured as biomass or count data, we have used the abundances of *year-1 fish* (recruitment). Our time series contain only a single age class, not an estimate of the population, and as a result, estimates of "population growth rates" (**A** in Equation 5) are actually estimates of the rates of change in recruitment. In addition, for most models, the use of one variate creates a single value for the species interaction matrix (**B** in Equation 5). For these models we have forgone analysis of these two components of MAR-1 processes, and have instead focussed on the covariate matrix (**C** in Equation 5), which estimates effects of covariates on a variate. For the

final model, we included all four species in a multivariate version of the model. As mentioned, this is a pilot study, to help scope out potential issues for future work.

DATA SOURCES

Time series of recruitment estimates were compiled from four recent stock assessments for exploited groundfish species off the coast of British Columbia and were used as the response variables (variates) in the MAR-1 analysis (Table A1). We selected these time series since they provided the relatively long, continuous time series required for MAR-1 analysis. In addition, we included five commonly cited abiotic factors to predict recruitment patterns described in the literature. Below are brief descriptions of time series for each species and covariate.

Pacific ocean perch (*Sebastes alutus*)

Pacific ocean perch (POP) supports the largest rockfish fishery in British Columbia, with an annual total allowable catch of 6,148 t (Edwards *et al.* 2011). POP are long lived, iteroparous and found at depths of around 150 – 300 m along the shelf and slope of the North Pacific from Honshu, Japan to San Diego, California (Love et al. 2002). As part of reproduction, females move to shallower inshore waters for insemination, after which they migrate deeper to the entrances of submarine gullies where they release larvae. Parturition (release of developed larvae by the mother) occurs between February and May, and larvae survival may depend on vertical upwelling or near shore currents to bring them to adult locations (Love et al. 2002). Therefore, it is possible that coastal upwelling has an effect on recruitment. Additionally, trends in recruitment may be positively related to climate regime shifts (Schnute et al. 2001).

Estimates for recruitment are measured as the number of year-1 fish and are available for Queen Charlotte Sound from 1940 to 2009 (Edwards *et al.* 2011; values used are the median estimates from the run 'Estimate *M* and *h*'). Over the past 69 years the median estimated recruitment for POP has been almost 20 million individuals per year (Figure 1). Two large recruitment events are evident over this time period; the 1953-54 event yielded an estimated 90 to over 120 million individuals per year, while the 1977 event, preceded by an abnormally low recruitment year, yielded a little less than an estimated 100 million individuals.

Canary rockfish (*S. pinniger*)

Canary rockfish are a commercially important species, with annual catches off the coast of British Columbia averaging approximately 900 t since 1945. Like POP, canary rockfish are long lived, with lifespans exceeding 80 years. They range from Shelikof Strait (western Gulf of Alaska) to Punta Colnett (northern Baja California) and are most common in depths between 80-200 m, but are known to occur from the intertidal to 838 m (Love et al. 2002). Recruitment estimates, measured as the number of year-1 fish, are available from 1940 to 2009 (Figure 1). Large-scale environmental changes owing to regime shifts or climate change may have an influence on canary rockfish productivity; however, empirical evidence to support this hypothesis is lacking (Stanley et al. 2009). Inter-annual variability in canary rockfish recruitment is small compared with POP. A substantial recruitment event occurred in 1999 that yielded an estimated three million individuals, and while recruitment declined between 1940 and the 1960s, the trend has since levelled off (DFO 2009).

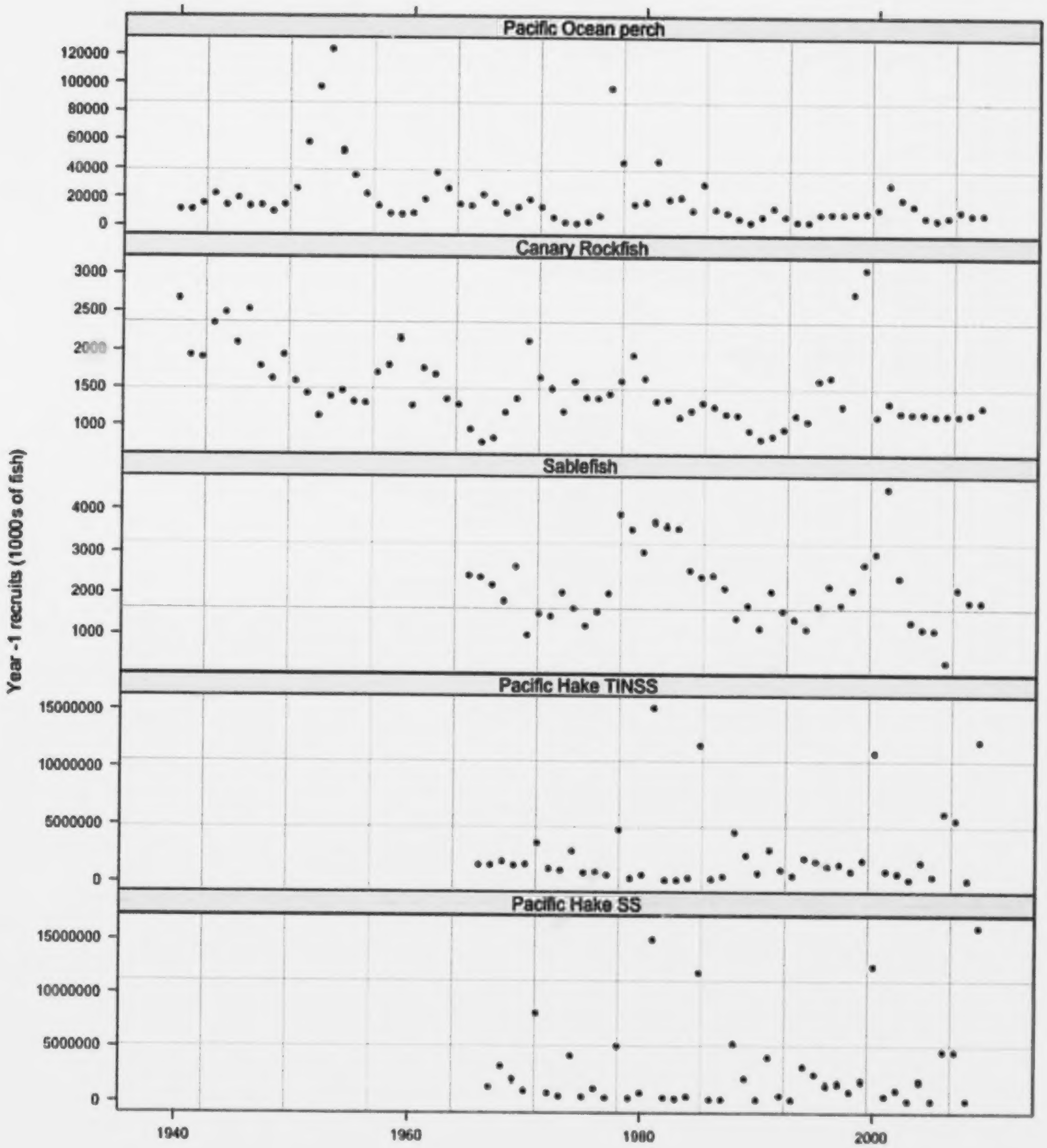

Figure 1. Time series plots of recruitment for the four species used in MAR-1 analysis in LAMBDA. Values are estimated medians from stock assessments, and for Pacific hake are given for both the TINSS and SS models (see text).

Sablefish (*Anoplopoma fimbria*)

Sablefish are a commercially important groundfish species, with an annual catch in Canadian waters averaging 4,500 t (http://www.canadiansablefish.com). Sablefish live on the shelf and slope from Japan and the Bering Sea to Baja California to depths greater than 1500 m. Production is thought to be influenced by decadal patterns in the Aleutian low and the associated regimes and regime shifts (Beamish et al. 1999a, Beamish et al. 1999b, King et al. 2000). Above average year classes occurred in years with warmer coastal sea-surface temperatures, increased frequency of south-westerly winds and intense Aleutian lows (King et al. 2000). Similar to POP, coastal upwelling is thought to influence recruitment; Schirripa and Colbert (2006) found that physical oceanographic variables within the California Current System have significant effects on recruitment of the west coast population of sablefish. Using a generalized additive model they found that sea level and Ekman transport explained over 70% of the variation in sablefish recruitment.

Annual recruitment estimates were predicted from the Beverton-Holt model (baseline assessment model), are measured as the number of year-1 fish, and are available between 1965 and 2009 (Cox et al. *in prep*). Between 1978 and 1983, recruitment estimates were higher than the preceding and following 12 years. In addition, a recruitment event occurred in 2001, yielding an estimated 4.5 million individuals (Figure 1).

Pacific hake (*Merluccius productus*)

Pacific hake, also known as Pacific whiting, are a semi-pelagic schooling species found along the west coast of North America, with a distribution generally between 25°N and 55°N. Coast-wide (Canadian and US waters) fisheries landings for Pacific hake have averaged 221 000 t annually between 1966 and 2010 (Stewart and Forrest 2011). The geographic distribution and local ecosystem role of hake vary annually in response to variability in environmental conditions. Adults tend to migrate farther north during the summer in relatively warm water years, compared with colder years. Recent research indicates that adult hake distribution may be more responsive to recent changes in temperature compared with historical periods, and that spawning may be occurring farther north (Phillips et al. 2007, Ressler et al. 2007).

Previous studies indicate that hake recruitment is negatively affected in cold-water years, when those conditions are associated with intense upwelling that moves water (and therefore larvae) away from inshore nurseries. Conversely, recruitment responds positively during warmer years (e.g. years of El Niño events), where reduced upwelling allows larvae to remain in favourable inshore nurseries (Bailey 1980, Bailey and Francis 1985, Hollowed and Bailey 1989).

Recruitment estimates, measured as the number of year-1 fish, are available between 1966 and 2011 (Figure 1). Pacific hake assessments are conducted jointly between the United States and Canada, and consequently, two models were generated to describe recruitment and biomass estimates, both deemed to be equally plausible (Stewart and Forrest 2011). There is little disagreement between the models (denoted SS [Stock Synthesis] and TINSS [This Is Not Stock Synthesis] for US and Canada, respectively), though the median estimates for SS show greater variability compared to TINSS. Large recruitment events for both time series are apparent in 1981, 1985 and 2000, with smaller recruitment events interspersed between larger events.

Abiotic factors

Recruitment dynamics of species along the Pacific coast are linked to regimes and regime shifts (Beamish et al. 2004). In our analysis, we used four commonly cited climate-ocean indices and one measure of sea-surface temperature. The five covariates included in the MAR-1 analysis are (full details of each are given in Appendix I):

a. Aleutian Low pressure index (ALPI), a measure of the intensity of winter weather in the North Pacific (Beamish et al. 1999a)
b. Upwelling index (UI), measured at 51°N 131°W, a monthly index of Ekman transport driven by geostrophic wind stress (data available at http://www.pfeg.noaa.gov)
c. Pacific Decadal Oscillation index (PDO), a monthly index that characterizes long-term fluctuations in sea-surface temperatures averaged over the North Pacific Ocean (Mantua et al. 1997)
d. Atmospheric Forcing Index (AFI), used to detect regime shifts by combining ALPI, PDO and the northwesterly atmospheric circulation anomalies for the North Pacific (averaged December through March) (McFarlane et al. 2000)
e. Sea-surface temperature (SST) time-series for the McInnes Island lighthouse (data available online[1])

Monthly values such as SST, UI and PDO were averaged over seasons such that "Winter" corresponds to January through March, "Spring" corresponds to April through June, "Summer" corresponds to July through September, and "Fall" corresponds to October through December. Although SST data were available for four lighthouses, Pearson correlation tests indicated that all four lighthouses were highly correlated (Appendix II). We selected the McInnes Island dataset based on its central location along the coast and because it had the greatest temporal overlap with the time series of abundance data (1955 – 2010).

MAR-1 ANALYSIS

For MAR-1 analysis in LAMBDA, we considered recruitment estimates as variates. All variables (excluding classification variables) were standardized to z-scores, so that coefficients were comparable across variables (Hampton et al. 2008). The z-score of an observation in a time series is a dimensionless quantity that indicates how many standard deviations the observation is above or below the mean of the time series (Whitlock and Schluter 2009), calculated as

$$\frac{\text{observation} - \text{mean}}{\text{standard deviation}}$$

To find the most likely parameters with the fewest possible interactions, we performed a combined iterative Conditional Least Squares (CLS) and Akaike's Information Criterion (AIC) search using LAMBDA. CLS parameter estimates are those that minimize the squared difference between the values of $\mathbf{X}_t$ predicted by the MAR-1 model, and the observed values of $\mathbf{X}_t$ (Ives et al. 2003). Each iterative search starts with random **B** and **C** matrices and cycles over the cells within the matrices, changing them one at a time. For each iteration, LAMBDA estimates **A**, **B** and **C** (Equation 5), as well as AIC for that model. AIC is a relative measure of how likely each model is given the data, and includes a penalty for inclusion of more variates (Box et al. 1994, Dennis et al. 1998, Burnham and Anderson 2002). At the end of the iterative CLS search, LAMBDA presents the model with the lowest AIC, which is thus concluded to be most supported

[1] http://www.pac.dfo-mpo.gc.ca/science/oceans/data-donnees/lighthouses-phares/index-eng.htm

Table 1. Descriptions of iterative CLS parameter searches implemented in LAMBDA

Model	Years	Variates	Covariates considered
1	1967 – 2009	All spp. recruitment estimates	None
2	1954 – 2004	POP(-1yr)	UI, PDO, SST, ALPI, AFI
3	1954 – 2004	Canary rockfish (-1yr)	UI, PDO, SST, ALPI, AFI
4	1965 – 2004	Sablefish (-1yr)	UI, PDO, SST, ALPI, AFI
5	1966 – 2004	Hake-TINSS model (-1yr)	UI, PDO, SST, ALPI, AFI
6	1967 – 2004	Hake-SS model (-1yr)	UI, PDO, SST, ALPI, AFI
7	1954 – 2003	POP	UI, PDO, SST, ALPI, AFI
8	1955 – 2006	Canary rockfish	UI, PDO, SST, ALPI, AFI
9	1965 – 2006	Sablefish	UI, PDO, SST, ALPI, AFI
10	1966 – 2006	Hake-TINSS model	UI, PDO, SST, ALPI, AFI
11	1967 – 2006	Hake-SS model	UI, PDO, SST, ALPI, AFI

by the data. Each model was bootstrapped to obtain 95% confidence limits for the coefficients included in the model. Coefficients whose confidence limits overlapped zero were dropped from the final best-fit model (Hampton et al. 2006, Hampton and Schindler 2006, Hampton et al. 2008).

We constructed one MAR model that included all species, but no covariates (Model 1), and ten additional models that included only one species, and a variety of covariates (Models 2-11, Table 1). We did not consider models with multiple species and covariates because performing an iterative search in LAMBDA using all variates and covariates would be very time-consuming (weeks to months) under current computing limitations. This is because the number of permutations for parameter arrangements in our model would have been 2^{350} (2^{25} possible combinations for the **B** matrix, and 2^{14} possible combinations for the **C** matrix, multiplied together equals 2^{350}). Additionally, in preliminary analyses we found a consistent lack of correlations between species and covariates (Appendix II).

For each species, we constructed two models, one in which covariates were lagged by one year, and one in which covariates were not lagged (Appendix III). We constructed lagged models to investigate the effect of covariates in year $t - 1$ on recruitment estimates for year t, as it is unclear which life stage (maternal stage prior to spawning, or the first year of life) determines recruitment success (Iles and Beverton 2000).

RESULTS

MAR-1 ANALYSIS

Species matrix

The first model examined covariances in recruitment among species on one another, irrespective of covariates. Of the 12 possible relationships between species, only two were significant (Table 2). Diagonal elements are interpreted as autocorrelation estimates. Both HakeSS and POP recruitments were positively correlated with sablefish recruitment (Table 2). Conditional R^2 values ranged between 0.20 and 0.71 for the model. Whether or not these results can be interpreted in a biological context remains to be determined, as this matrix effectively finds the effect of one species on another species per-capita recruitment growth rate.

Table 2. Iterative CLS search (n = 70,000 iterations, bootstraps = 100,000) estimates of the coefficients of the matrix B (with 95% confidence limits) for significant interactions for model 1. Autocorrelation estimates are given on the diagonal; † indicates values that are not significantly different from zero (the confidence intervals include 0).

	POP	Canary rockfish	Sablefish	HakeSS
POP	0.53[0.19,0.83]			
Canary rockfish		0.45[0.15,0.69]		
Sablefish	0.36[0.02,0.70]		0.23[-0.06,0.52]†	0.25[0.01,0.52]
HakeSS				-0.42[-0.67,-0.12]
Conditional R^2	0.2018	0.2626	0.4177	0.7126

Pacific ocean perch

Both lagged and non-lagged models for POP included abiotic variables that were statistically significant (Table 3). In non-lagged models, PDO in the fall and ALPI had strong positive effects on recruitment, while PDO in the summer and AFI had negative effects on recruitment. In lagged models, UI in the winter had a negative relationship with recruitment, while UI in the spring had a positive effect. Conditional R^2 values indicate that the covariates included explain 51% of the variation in recruitment for the non-lagged model, and 44% of the variation in recruitment for the lagged model (Table 3).

Significant interaction in lagged and non-lagged models in our analysis for POP suggests that effects of environmental variability on maternal condition and the first year of life may be important for recruitment success for this species, which is in line with previous studies that have indicated that it is unknown at what early life-history stage POP recruitment is determined (Iles and Beverton 2000). It is not clear why significant interactions were observed in either lagged or unlagged models (but not in both) for the other species in our analysis. While not investigated, it is possible that longer lags also show an effect.

The coefficients included for both models are not unexpected, given that previous studies have suggested that POP recruitment is affected by upwelling and regime shifts (Love et al. 2002). In particular, the relationships between upwelling and recruitment in the year-lagged model correspond to when parturition would be taking place. Additionally, AFI in the non-lagged model, which is used to detect regime shifts, has a strong relationship with recruitment. This relationship possibly indicates that enhanced maternal condition occurs during periods of intense Aleutian lows, above-average frequency of westerly and south-westerly winds, and cooling of sea surface temperatures in the central North Pacific (McFarlane et al. 2000).

Canary rockfish

No significant relationships were apparent in either the lagged or non-lagged models for canary rockfish recruitment. Conditional R^2 values for both models indicate that the model explains ~30% of the variance in recruitment estimates (Table 3). As there is no empirical evidence linking canary rockfish recruitment to ocean-climate regimes or regime shifts, these results are not unexpected. In addition, it is possible that there are no significant relationships for canary rockfish because variability within the time series is not very large (Figure 1). There are no large recruitment events or abnormally low years. When compared to hake, whose annual recruitment varied between the low millions to over 15 billion individuals, canary recruitment is relatively stable (varying between one and four million fish annually).

Table 3. Iterative CLS search (n = 33,000 iterations, bootstraps = 5000) parameter estimates with 95% confidence limits values for significant interactions for models 2 to 11. Autocorrelation estimates denoted † are not significantly different from zero.

Species	POP	Canary Rockfish	Sablefish	HakeTINSS	HAKESS
	Parameter estimates				
Covariate					
Non-lagged					
SST winter					
SST spring			-0.59 [-1.15,-0.03]		
SST summer					
SST fall					
ALPI	0.62 [0.16,1.05]				
PDO winter					
PDO spring					
PDO summer	-0.36[-0.68,-0.02]				
PDO fall	0.72 [0.18,1.28]				
UI winter					
UI spring					
UI summer					
UI fall			-0.24 [-0.46,-0.02]		
AFI	-0.86[-1.58,-0.15]				
Autocorrelation	0.58 [0.35,0.75]	0.44 [0.12,0.72]	0.34 [-0.01,0.65]†	-0.25[-0.59,0.14]†	-0.30[-0.65,0.07]†
Conditional R^2	0.5135	0.3140	0.5336	0.6570	0.7378
Lagged					
SST winter					
SST spring					
SST summer					
SST fall					
ALPI					0.78[0.01,1.52]
PDO winter					
PDO spring					1.02[0.31,1.77]
PDO summer				-0.56 [-1.11,-0.02]	
PDO fall					
UI winter	-0.24 [-0.47,-0.02]				-0.58[-1.05,-0.11]
UI spring	0.23 [0.00,0.45]				
UI summer					
UI fall					
AFI					-1.72[-2.92,-0.60]
Autocorrelation	0.54 [0.27,0.75]	0.49 [0.17,0.74]	0.52 [0.11,0.84]	-0.36[-0.068,0.00]	-0.59[-0.81,-0.29]
Conditional R^2	0.4436	0.3206	0.1831	0.7039	0.8147

Sablefish

For sablefish, we expected there to be positive relationships with strong ALPI and UI, and warmer SST based on previous studies (Beamish et al. 1999a, Beamish et al. 1999b, King et al. 2000, Schirripa and Colbert 2006). Both UI in the fall and SST in the spring had negative relationships with recruitment in the non-lagged model. This differs from POP which had negative and positive relationships with UI (positive in spring, negative in the winter), and no relationship with SST. In addition, there was no relationship with ALPI (Table 3). It is unclear why there was no effect of ALPI on sablefish recruitment.

Hake

For hake, we expected there to be a relationship between PDO, SST and UI based on previous studies (Bailey, 1980; Bailey and Francis, 1985; Hollowed and Bailey, 1989). Interestingly, there is a considerable difference between parameter estimates for the two lagged models using the two recruitment estimates for hake (Table 3) even though recruitment estimates

for the two time series for hake are highly correlated (Pearson coefficient = 0.93). There was only one significant relationship between recruitment and abiotic factors for Canadian derived HakeTINSS, with PDO in the summer having a negative relationship with lagged recruitment. In contrast, there are significant relationships between four covariates and the US-derived HakeSS. Both PDO in the spring and ALPI have positive relationships with lagged recruitment, and AFI and UI in the winter have negative relationships. It is possible the greater overall variability in HakeSS (S.E. = 5.78×10^5) compared to HakeTINSS (S.E. = 5.11×10^5) affected the relationships.

For the non-lagged model, no significant relationships were observed between recruitment and abiotic factors and autocorrelation coefficients were zero. Conditional R^2 values were between 0.30 and 0.81 for all hake models.

CONCLUSIONS AND RECOMMENDATIONS

While there are similarities between published hypotheses for drivers of recruitment and our outputs from LAMBDA for the species investigated, we are apprehensive in making generalizations about the usefulness of the LAMBDA software as our inputs are recruitment time series.

BENEFITS AND LIMITATIONS OF LAMBDA

LAMBDA is an open source MatLab toolkit that fits MAR-1 models to multi-species time series data (although it does not require the user to use MatLab). One of the main advantages of LAMBDA is that it carries out all calculations for MAR-1 analysis. The data requirements are uncomplicated, continuous time-series data are all that are needed. In terms of formatting, data can be imported as an Excel spreadsheet, and subsequently saved in LAMBDA format. Within LAMBDA, data can be divided into subsets or transformed, and data can also be simulated. Once analysis is complete, datasets can be exported as comma separated values, or text files. Additionally, results of MAR-1 analysis can be saved to be examined later thereby avoiding repeating the iterative CLS search.

The manual for LAMBDA adequately describes procedures for formatting, saving and exporting data, as well as the mechanics of MAR-1 models. However, information on assessing the fit of the model and interpretation of the coefficients is lacking. There is no explicit description on how to determine how many iterations or bootstraps to perform, both of which have a considerable impact on the validity of the model. Too few iterations would not cover all possible permutations of the matrices, possibly missing the most parsimonious model (that which has the lowest AIC), too few bootstraps would lead to inaccurate confidence limits. In addition, computing time for the iterative CLS parameter search increases drastically as more variates and covariates are included, which could cause issues for those interested in fitting complex models.

The executable version of LAMBDA has the considerable advantage of being free, but at the same time might limit what the user is capable of exploring. It may be possible within MatLab to run loops to shorten the iterative search process (Hampton et al. 2006, Hampton et al. 2008). Additionally, normality tests of the residuals are one way to assess the fit of the model (Ives et al. 2003), but are not available in the free executable version of LAMBDA.

Of particular concern for this study are the substantial differences between estimated coefficients for HakeTINSS and HakeSS, which indicate that relatively small changes to a dataset

can change results dramatically. All recruitment estimates used in our analysis were median values taken from model outputs, and have associated confidence intervals, some of which were large (mid-century estimates for POP and early 2000's estimates for all species have very wide confidence intervals). This means that the 95% confidence limits calculated by bootstrap resampling should be adjusted to account for uncertainty in recruitment estimates, something that is beyond the capabilities of LAMBDA.

Finally, the developers are no longer actively working on LAMBDA, although software packages currently under development, including the MARSS R package (available online[2]) are attempting to address the limitations of LAMBDA.

FUTURE AVENUES FOR EXPLORATION

Preliminary investigations of recruitment time series yielded promising results that warrant further investigation. An alternative to using recruitment time series for implementing MAR-1 processes would be to use estimates of spawning stock biomass, which are available for the species investigated in this pilot study. Considerably more complicated models are required to do this, as the inclusion of factors including fishing effort and confidence intervals for biomass estimates would require a state-space approach.

Models that differentiate process and observation/assessment errors are being developed for fisheries science; state-space models have already been used to examine trends in rockfish population assemblages (Berntson et al. 2008). Unfortunately, these models are not easily generated using currently available freeware. The MARSS R package (released in 2010 and still actively updated) fits constrained and unconstrained linear multivariate autoregressive state-space (MARSS) models to multivariate time series data. The package uses a state-space approach and should eventually allow for the incorporation of known catches from fisheries into the model (Eric Ward, NOAA, pers. comm.).

For potential future studies, we recommend reviewing the literature summarised here, plus any subsequent studies (a search on the Ives et al. 2003 paper, using ISI Web of Science, found 87 publications that have cited the article since publication). Investigating the progress and capabilities of the R package MARSS is recommended (given the limitations of LAMBDA).

[2] http://cran.r-project.org/web/packages/MARSS/index.html

LITERATURE CITED

Bailey, K. M. 1980. Recent changes in the distribution of hake larvae: causes and consequences. CalCOFI Reports:167-171.

Bailey, K. M., and Francis, R. C. 1985. Recruitment of Pacific whiting, *Merluccius productus*, and the ocean environment. Marine Fisheries Review **47**:8-14.

Beamish, R. J., Benson, A. J., Sweeting, R. M., and Neville, C. M. 2004. Regimes and the history of the major fisheries off Canada's west coast. Progress in Oceanography **60**:355-385

Beamish, R. J., McFarlane, G. A., and Thomson, R. E. 1999a. Recent declines in the recreational catch of coho salmon (Oncorhynchus kisutch) in the Strait of Georgia are related to climate. Canadian Journal of Fisheries and Aquatic Sciences **56**:506-515.

Beamish, R. J., Noakes, D. J., McFarlane, G. A., Klyashtorin, L., Ivanov, V. V., and Kurashov, V. 1999b. The regime concept and natural trends in the production of Pacific salmon. Canadian Journal of Fisheries and Aquatic Sciences **56**:516-526.

Berntson, E., Cope, J., Drake, J., Gustafson, R., Holmes, E., Levin, P., Tolimieri, N., Waples, R., and Sogard, S. 2008. Preliminary Scientific Conclusions of the Review of the Status of 5 Species of Rockfish: Bocaccio (*Sebastes paucispinis*), Canary Rockfish (*Sebastes pinniger*), Yelloweye Rockfish (*Sebastes ruberrimus*), Greenstriped Rockfish (*Sebastes elongatus*) and Redstripe Rockfish (*Sebastes proriger*) in Puget Sound, Washington. Northwest Fisheries Science Center,National Marine Fisheries Service, Seattle.

Box, G. E. P., Jenkins, G. M., and Reinsel, G. C. 1994. Time series analysis: forecasting and control. Prentice Hall, Englewood Cliffs, New Jersey, USA.

Burnham, K. P., and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer, New York, New York, USA, 488 p.

De Valpine, P., and Hastings, A. 2002. Fitting population models incorporating process noise and observation error. Ecological Monographs **72**:57-76.

Dennis, B., Kemp, W. P., and Taper, M. L.1998. Joint density dependence. Ecology **79**:426-441.

Dennis, B., Ponciano, J. M., Lele, S. R., Taper, M. L., and Staples, D. F. 2006. Estimating density dependence, process noise, and observation error. Ecological Monographs **76**:323-341.

DFO. 2009. Recovery assessment of canary rockfish in British Columbia waters. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2009/041.

Edmondson, W. T. 1994. Sixty Years of Lake Washington: a Curriculum Vitae. Lake and Reservoir Management **10**:75-84.

Edwards, A.M., Starr, P.J. and Haigh, R. 2011. Stock assessment for Pacific ocean perch (*Sebastes alutus*) in Queen Charlotte Sound, British Columbia. Canadian Science Advisory Secretariat, Research Document 2011/111.

Hampton, S. E., Izmest'eva, L. R., Moore, M. V., Katz, S. L., Dennis, B., and Silow, E. A. 2008. Sixty years of environmental change in the world's largest freshwater lake - Lake Baikal, Siberia. Global Change Biology **14**:1947-1958.

Hampton, S. E., Scheuerell, M. D., and Schindler, D. E. 2006. Coalescence in the Lake Washington story: Interaction strengths in a planktonic food web. Limnology and Oceanography **51**:2042-2051.

Hampton, S. E., and Schindler, D. E. 2006. Empirical evaluation of observation scale effects in community time series. Oikos **113**:424-439.

Hollowed, A. B., and Bailey, K. M. 1989. New perspectives on the relationship between recruitment of Pacific hake and the ocean environment. Pages 207-220 *in* R. J. Beamish and G. A. McFarlane, editors. Effects of Ocean Variability on Recruitment and an Evaluation of Parameters Used in Stock Assessment Models. Canadian Special Publication of Fisheries and Aquatic Sciences, 108.

Holmes, E. E. 2001. Estimating risks in declining populations with poor data. Proceedings of the National Academy of Sciences of the United States of America **98**:5072-5077.

Iles, T. C., and Beverton, R. J. H. 2000. The concentration hypothesis: the statistical evidence. Ices Journal of Marine Science **57**:216-227.

Ives, A. R. 1995a. Measuring resilience in stochastic systems. Ecological Monographs **65**:217-233.

Ives, A. R. 1995b. Predicting the response of populations to environmental change. Ecology **76**:926-941.

Ives, A. R., Dennis, B., Cottingham, K. L., and Carpenter, S. R. 2003. Estimating community stability and ecological interactions from time-series data. Ecological Monographs **73**:301-330.

King, J. R., McFarlane, G. A., and Beamish, R. J. 2000. Decadal-scale patterns in the relative year class success of sablefish (Anoplopoma fimbria). Fisheries Oceanography **9**:62-70.

Lindegren, M., Mollmann, C., Nielsen, A., and Stenseth, N. C. 2009. Preventing the collapse of the Baltic cod stock through an ecosystem-based management approach. Proceedings of the National Academy of Sciences of the United States of America **106**:14722-14727.

Lindley, S. T. 2003. Estimation of population growth and extinction parameters from noisy data. Ecological Applications **13**:806-813.

Love, M. S., Yoklavich, M., and Thorsteinson, L. 2002. The Rockfishes of the Northeast Pacific. University of California Press, Berkeley and Los Angeles, 404 p.

Mac Nally, R., Thomson, J. R., Kimmerer, W. J., Feyrer, F., Newman, K. B., Sih, A., Bennett, W. A., Brown, L., Fleishman, E., Culberson, S. D., and Castillo, G. 2010. Analysis of pelagic species decline in the upper San Francisco Estuary using multivariate autoregressive modeling (MAR). Ecological Applications **20**:1417-1430.

Mantua, N. J., Hare, S. R., Zhang, Y., Wallace, J. M., and Francis, R. C. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society **78**:1069-1079.

McFarlane, G., King, J., and Beamish, R. 2000. Have there been recent changes in climate? Ask the fish. Progress in Oceanography:147-169.

Neubert, M. G., and Caswell, H.. 1997. Alternatives to resilience for measuring the responses of ecological systems to perturbations. Ecology **78**:653-665.

Phillips, A. J., Ralston, S., Brodeur, R. D., Auth, T. D., Emmett, R. L., Johnson, C., and Wespestad, V. G. 2007. Recent pre-recruit Pacific hake (Merluccius productus) occurrences in the northern California current suggest a northward expansion of their spawning area.CalCOFI Reps. **48**:215-229.

Ressler, P. H., Holmes, J. A., Fleischer, G. W., Thomas, R. E., and Cooke, K. C. 2007. Pacific hake, Merluccius productus, autecology: a timely review Mar. Fish. Rev. **69**:1-24.

Schirripa, M. J., and Colbert, J. J. 2006. Interannual changes in sablefish (Anoplopoma fimbria) recruitment in relation to oceanographic conditions within the California Current System. Fish. Ocean. **15**:25-36.

Schnute, J. T., Haigh, R., Krishka, B. A., and Starr, P. 2001. Pacific Ocean Perch Assessment for the West Coast of Canada in 2001.Can. Sci. Adv. Sec. Res. Doc. 2002/138. 96 pp.

Stanley, R. D., Starr, P., and Olsen, N. 2009. Stock assessment for Canary rockfish (Sebastes pinniger) in British Columbia waters. DFO Can. Sci. Advis. Sec. Res. Doc. xxii + 198 pp.

Stewart, I. J., and Forrest, R. E. 2011. Status of the Pacific Hake (Whiting) stock in U.S. and Canadian Waters in 2011. Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, WA.

Viscido, S. V. 2007. LAMBDA Long-term Assemblage MAR(1)-Based Data Analysis. Northwest Fisheries Science Centre, Seattle.

Viscido, S. V., and Holmes, E. E. 2010. Statistical modelling of communities and ecosystems using the LAMDA software tool. Environmental Modelling & Software **25**:1905-1908.

Whitlock, M.C., and Schluter, D. 2009. The Analysis of Biological Data. Roberts and Company Publishers, Greenwood Village, Colorado. 700pp.

Ward, E. J., Chirakkal, H., Gonzalez-Suarez, M., Aurioles-Gamboa, D., Holmes, E. E., and Gerber, L. 2010. Inferring spatial structure from time-series data: using multivariate state-space models to detect metapopulation structure of California sea lions in the Gulf of California, Mexico. Journal of Applied Ecology **47**:47-56.

APPENDIX I

MAR-1 MODEL PARAMETER DETAILS

Table A1 Descriptions of variates and covariates used in MAR-1 analysis

Variable	Description	Years	Number of series
Pacific ocean perch (POP)	Posterior medians for Est M&h model in Figure 5 of draft POP 2010 assessment (Edwards et al. 2011)	1940 – 2010	1
Canary rockfish	Model 11 (preferred run) posterior medians for recruitment from the 2009 Canary Rockfish assessment (DFO 2009)	1940 – 2009	1
Hake	TINSS – stands for "This is not Stock Synthesis" and are the recruitment estimates from an age-structured model that is conditioned on historical catch and parameterized from a management-oriented perspective, where leading estimated parameters are *MSY* and F_{MSY}. (Stewart and Forrest 2011)	1966 – 2011	1
	SS – stands for "Stock Synthesis" and are estimates that use the modeling framework developed by Dr. Richard Methot at the NWFSC (Stewart and Forrest 2011)	1966 – 2011	1
Sablefish	Age-1 recruits as predicted from the Beverton-Holt model (Cox et al. *in prep*)	1965 – 2010	1
McInnes Island lighthouse	52°16'N 128°43'W Monthly sea surface temperature averaged into four seasons: "Winter" (January-March), "Spring" (April-June), "Summer" (July-September), "Fall" (October-December) (*data available online*)[3]	1955 – 2006	4
Upwelling Index (UI)	51°N 131°W Monthly indices based on estimates of offshore Ekman transport driven by geostrophic wind stress averaged into four seasons: "Winter" (January-March), "Spring" (April-June), "Summer" (July-September), "Fall" (October-December) (*data available online*)[4]	1946 – 2009	4
Pacific Decadal oscillation (PDO)	Characterizes long-term fluctuations of the average North Pacific sea surface temperature (Manthua et al. 1997). A reflection of sea surface temperatures in the Pacific basin. During positive phases of the PDO the west coast of North America warms while the central Pacific experiences cooling. The opposite occurs for a negative PDO. PDO was averaged into four seasons: "Winter" (January-March), "Spring" (April-June), "Summer" (July-September), "Fall" (October-December)	1940 – 2009	5
Aleutian Low Pressure Index (ALPI)	This index measures the relative intensity of the Aleutian Low pressure system of the north Pacific (December through March). It is calculated as the mean area (km^2) with sea level pressure $\leq$ 100.5 kPa and expressed as an anomaly from the 1950-1997 mean. A positive index value reflects a relatively strong, or intense Aleutian Low (Beamish et al. 1999b)	1940 – 2008	1
Atmospheric Forcing Index (AFI)	Utilizes standardized scores of the first component from a principal components analysis on the Aleutian Low Pressure Index, Pacific Interdecadal Oscillation Index and the northwesterly atmospheric	1900 – 2004	1

[3] http://www.pfeg.noaa.gov

[4] http://www.pac.dfo-mpo.gc.ca/science/oceans/data-donnees/lighthouses-phares/index-eng.htm

circulation anomalies for the North Pacific (December through March). Positive values represent intense Aleutian lows, above average frequency of westerly and southwesterly winds, cooling of sea surface temperatures in the central North Pacific, and warming within North American coastal waters (McFarlane et al. 2000).

APPENDIX II

CORRELATION TESTS BETWEEN VARIABLES

We tested time series for all the variates and covariates against one another to determine the degree of correlation between them. We were interested in their relationship to see if the MAR-1 analysis in LAMBDA yielded the same results.

In addition, we tested time series for the four lighthouses against one another to determine the degree of correlation between them.

Methods

A .csv file with all time series was imported into R and the following code was used to construct panel plots that contained histograms of the data, Pearson correlation coefficients as well as scatterplots with linear regressions.

Code for figures for correlation tests

```
panel.hist <- function(x, ...)
{ usr <- par("usr"); on.exit(par(usr))
par(usr = c(usr[1:2], 0, 1.5) )
h <- hist(x, plot = FALSE)
breaks <- h$breaks; nB <- length(breaks)
y <- h$counts; y <- y/max(y)
rect(breaks[-nB], 0, breaks[-1], y, col="cyan", ...)
}
panel.blank <- function(x, y)
{ }
panel.cor <- function(x, y, digits=3, prefix="",
cex.cor,cheese="pairwise.complete.obs")
{
usr <- par("usr"); on.exit(par(usr))
par(usr = c(0, 1, 0, 1))
r <- cor(x, y,use=cheese)
txt <- format(c(r, 0.123456789), digits=digits)[1]
txt <- paste(prefix, txt, sep="")
if(missing(cex.cor)) cex <- 0.6/strwidth(txt)
#text(0.5, 0.5, txt, cex = cex * r)
text(0.5, 0.5, txt, cex = cex)
}
panel.dots<-
function (x, y, col = par("col"), bg = NA, pch = par("pch"),
    cex = 1, col.abline = "red", span = 2/3, iter = 3, ...)
{
    points(x, y, pch = ".", col = col, bg = bg, cex = cex)
    ok <- is.finite(x) & is.finite(y)
    if (any(ok))
    r<-lm(x[ok]~y[ok])
    abline(r,col=col.abline)
        #lines(stats::lowess(x[ok], y[ok], f = span, iter = iter),
            #col = col.smooth, ...)
}
pplot<-function(x,lower.panel=lower.panel,upper.panel=upper.panel,
  diag.panel=diag.panel,gap=gap,...){
    windows(8.5,11)
    pairs(x, lower.panel=panel.dots,
    upper.panel=panel.cor, diag.panel=panel.hist,gap=0)
  }
```

Table A2. Pearson correlation coefficients between species and between species and covariates used in LAMBDA MAR models

Species	POP	Canary Rockfish	Sablefish	HakeTINSS	HakeSS
			Parameter estimates		
POP	-	0.109	0.532	0.0335	0.0854
Canary Rockfish	-	-	0.147	-0.00746	0.075
Sablefish	-	-	-	-0.108	0.0209
HakeTINSS	-	-	-	-	0.933
HakeSS	-	-	-	-	-
Covariate					
Non-lagged					
SST winter	0.166	0.0579	0.043	-0.0402	-0.0866
SST spring	-0.169	-0.0808	-0.148	-0.155	-0.217
SST summer	-0.0497	0.0684	0.0113	-0.235	-0.147
SST fall	0.0085	-0.0399	0.212	-0.154	-0.0687
ALPI	0.0965	0.199	0.161	-0.191	-0.241
PDO winter	-0.0524	0.100	0.0558	-0.245	-0.294
PDO spring	-0.154	0.0837	0.0261	-0.133	-0.190
PDO summer	-0.201	-0.118	0.0449	-0.211	-0.192
PDO fall	-0.0815	-0.0428	0.190	-0.198	-0.101
UI winter	-0.00554	0.079	-0.177	-0.0338	-0.137
UI spring	0.140	-0.106	0.0764	0.140	0.136
UI summer	-0.204	0.0684	-0.131	0.101	0.077
UI fall	-0.261	-0.0399	-0.203	-0.107	-0.155
AFI	-0.0137	0.186	0.120	-0.191	-0.241
Lagged					
SST winter	0.120	-0.0405	0.193	0.206	0.289
SST spring	-0.153	0.129	-0.170	0.140	0.145
SST summer	-0.035	0.126	-0.0926	-0.0194	-0.0288
SST fall	0.078	0.194	-0.0285	-0.108	-0.0993
ALPI	-0.0326	0.191	0.104	0.0769	-0.0583
PDO winter	-0.177	0.143	0.0692	0.103	0.187
PDO spring	-0.205	0.198	-0.0606	-0.0062	0.0315
PDO summer	-0.274	-0.00734	-0.112	-0.264	-0.275
PDO fall	-0.127	0.0411	-0.0362	-0.277	-0.329
UI winter	-0.0623	-0.101	-0.249	0.078	0.0935
UI spring	0.0905	0.0768	-0.0293	0.0381	0.0571
UI summer	-0.245	0.0599	-0.206	0.054	-0.061
UI fall	-0.265	-0.0381	-0.147	0.094	-0.329
AFI	-0.114	0.171	0.135	0.0769	0.133

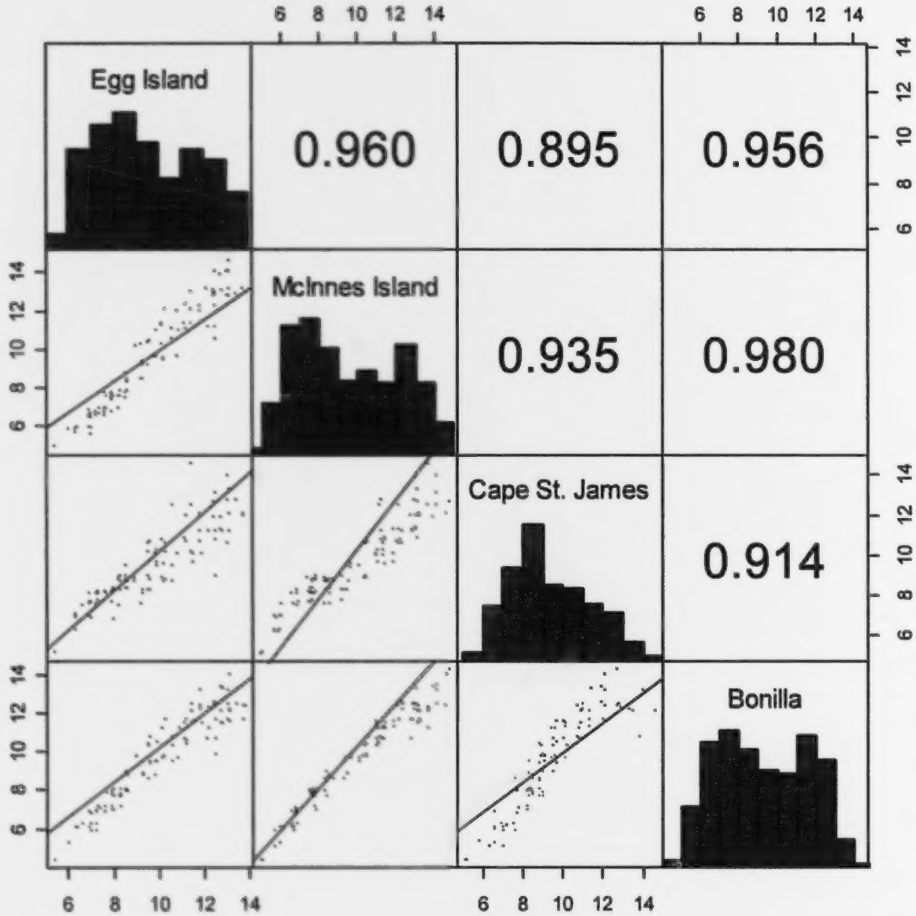

Figure A1. Histograms of time series, Pearson correlation coefficients and scatterplots for the four lighthouse time series.

APPENDIX III

QUICK PROCEDURE FOR MAR-1 ANALYSIS IN LAMBDA

Below is the procedure used for MAR-1 analysis in this Technical report. Please refer to the LAMBDA manual (Viscido 2007) for more detailed instructions.

1. Create an .xls file of the desired dataset. Make sure there are **no missing values** in any of the columns. The dataset should have at least one classification variable (e.g. month, year), at least one variate, and any desired covariates

2. Open LAMBDA. Load dataset by clicking File → Import data → From MS Excel file… → choose file → OK

3. Format data. Click Statistics → Transform the data → Natural logarithm → under variables choose "Variates". Next, click Statistics → Transform the data → Z-score → select "All" → OK

4. Save formatted dataset. This is done in case the data needs to be re-examined later, and saves having to format again. Click File → Save Data as… → file_name.dst

5. Determine which parameters to use. In the menu bar click MAR-1 → CLS Parameter estimation → CLS Search over State Space for which interactions to use → under number of iterations select according to description below → OK → Select Criterion to use → AIC → OK. At this point, it will look like the software has crashed since the LAMBDA pane is frozen; to confirm that the search is being performed, look at the command window, after "Starting CLS Estimates" the three dots should be flashing. Closing LAMBDA prior to the completion of the run will cause LAMBDA to crash.

Selecting the appropriate number of iterations – the goal of performing the CLS search is to find the best model out of all the models, therefore, the total number of iterations should be greater than or equal to the total number of permutations. To determine this, count the number of coefficients present in each matrix (both B and C), add them together, and calculate two to the power of this value. Keep in mind that a large number of iterations can take a considerable amount of time

6. Once the iterative search is complete, run MAR-1 analysis. In the menu bar, click
   MAR-1 → Run MAR-1 model with CLS Estimates →
   MAR-1 → Assess model fit →
   MAR-1 → Bootstrap the model → select desired number of bootstraps →
   MAR-1 → Compute 95% confidence limits →
   MAR-1 → View confidence limits → Significant interactions → select "No" when prompting about writing to a file

7. Save MAR-1 results. File → MAR → Save MAR results

8. Clear MAR-1 results prior to commencement of new analysis. Data → Clear Data
   MAR-1 → Clear MAR-1 Estimates